ELSEVIER

Journal of Archaeological Science 34 (2007) 1677–1684

Journal of Archaeological SCIENCE

http://www.elsevier.com/locate/jas

Ascertaining an agent: using tooth pit data to determine the carnivore/s responsible for predation in cases of suspected big cat kills in an upland area of Britain

Ros Coard*

Department of Archaeology and Anthropology, University of Wales Lampeter, Lampeter, Ceredigion, Wales, SA48 7ED, UK

Received 26 August 2006; received in revised form 1 December 2006; accepted 5 December 2006

Abstract

The identification of the involvement of a particular carnivore in the modification of bone assemblages concerns a number of fields of research including archaeological and palaeontological enquiry. Taphonomy provides a methodology by which bone assemblages can be analysed and interpreted and this is more often undertaken with archaeological or palaeontological assemblages. A taphonomic analysis is undertaken here in order to determine the perpetrator of predation attacks on domestic stock from a modern-day setting. Recently reported techniques using tooth marks preserved on bone surfaces made by known carnivores are successful at determining some class sizes of predators and are used here to determine the perpetrator(s). Although a class size of carnivore is readily identified by this methodology, a particular carnivore taxon is not. Tooth morphology and dental configuration are reported here as better criteria for identifying a particular taphonomic agent. Tooth pit dimensions are used here to identify the class size of carnivores involved, and tooth morphology and cusp spacing to suggest a medium sized felid and fox as taphonomic agents. The identification of the medium-sized felid may support observations and reports of alleged ''big'' cat kills in the area. The study has important implications for the interpretation of fossil sites where felids may have been involved in the modification of animal carcasses but are archaeologically invisible in terms of their fossil remains.
© 2006 Elsevier Ltd. All rights reserved.

Keywords: Carnivore; Taphonomic agent; Predation; Tooth pits; Carnassials; Tooth morphology

1. Introduction

Accounts by local farmers and livestock owners of large cat predation on animal stocks along with sightings of ''big'' cats, occur in the rural areas of West Wales on an almost cyclical annual basis. Accounts and sightings are more frequently reported by the local press during the winter months and especially after a few days of sharp frost, snow and/or other extreme weather conditions. The context of the killings and sightings are imperfectly understood for this area in as much as that the predators have not been positively identified to any taxonomic level, it is unclear how many predators there are and it remains unclear how many wild or even owned animals are predated upon in any given year. Equally, the economic as well as social and psychological impact of such losses on the local community is undetermined and poorly understood. This paper seeks to apply a methodology by which the predator/s may be identified by the zooarchaeological and taphonomic study of some of the partial animal remains left from alleged large predator attacks.

Establishing the identity and number of the perpetrator/s in an instance of predation is the concern of a wide number of researchers and the effects of such an attack impinge on a wide number of research issues. These interests are reflected in, for example, conservation studies (Carbone and Gittleman, 2002; Ginsberg and Macdonald, 1990; Mishra, 1997; Oli et al., 1994), in ecology (Meriggi and Lovari, 1996; Ranta et al., 1999; Stahl et al., 2002), issues relating to introductions,

* Corresponding author.
E-mail address: r.coard@lamp.ac.uk

0305-4403/$ - see front matter © 2006 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jas.2006.12.006

reintroductions or extinctions (Berger et al., 2001; Sinclair et al., 2003; Wilson, 2004), land and stock management (Roberts, 1986), the forensic sciences (Haglund, 1997; Rothwell et al., 2001; Vogel et al., 2000) as well as palaeoecological, archaeological and palaeoanthropological enquiry (Boaz et al., 2004; Domínguez-Rodrigo, 1999; Dyan et al., 2002; de Ruiter and Berger, 1999; Selvaggio and Wilder, 2001; Treves and Naughton-Treves, 1999; and extensive references within all of these texts). Central to the interpretation or assignation of a particular predator being responsible is the taphonomic analysis of any surviving skeletal or soft tissue material. In present-day settings carnivores can be observed or experienced directly (Domínguez-Rodrigo, 1999; Wilson, 2004). In an archaeological or palaeoanthropological context, the perpetrators are not observable, leaving any inferences made being based on other established methodologies. The application of taphonomy as a methodology by which to explore such problems has a focused research history within the archaeological literature and it is not the intent to recount this here. The intent of this paper is to see if by using a taphonomic analysis centred on tooth pit data, the carnivores responsible for recent attacks on domestic animals within the study area can be determined. In these particular cases there are the surviving animal carcasses but no independent or verifiable data, such as scats, recoverable DNA, trip camera images etc. are available with the exception of some possible fibres.

The aim of this paper is to establish if taphonomic analyses can successfully identify a particular species of carnivore as the cause of bone damage. The converse of this stated aim, a taphonomic analysis being carried out but the agent of destruction failing to be identified, may also be possible. If this proves to be the case then the interest lies in whether this is due to the failure of the methodology to identify species or due to other factors such as taphonomic overprinting. The archaeological literature documents some attempts to address this issue with regards to tooth pit data for which a *modus operandi* is developing but as yet the implications and interpretations have not proved definitive (see for example Selvaggio and Wilder, 2001 and for contra Domínguez-Rodrigo and Piqueras, 2003).

2. Study area and sample

The study area is the rural landscape to the west of the Cambrian Mountains in West Wales, U.K. (see Fig. 1). The area is typified by unimproved grasslands and pasture lands as well as land given over to agriculture, commercial and mineral developments. The area contains significant upland rising to 753 m, much of which is grazed and woodland habitats. Equally, it is noted for its outstanding natural beauty and is therefore a vital tourist and heritage resource. Reports of large predator activity emanate from villages and hamlets closest to the western flanks of the Cambrian Mountains down to the Brechfa Forest at its southern limits (see Fig. 2). The area is noted for some large raptors, particularly the red kite (*Milvus milvus*) and the buzzard (*Buteo buteo)* and smaller mammalian carnivores, such as fox (*Vulpes vulpes*), the mustelids, including stoat (*Mustela erminea*), weasel (*Mustela nivalis*), polecat (*Mustela putorius*), mink (*Mustela vison*), badger (*Meles meles*), and otter (*Lutra lutra*). The status of the pine marten (*Martes martes*) in the area is unclear in that it may be present but is certainly very rare (Lucas, 1997). Feral cats and dogs are ubiquitous. The area lacks any other form of larger native carnivores.

The study sample consists of carcasses of four sheep and a foal, identified as Carcasses 1–5, all in various states of completeness. The carcasses of one sheep (Carcass 1) and the foal (Carcass 2) had been abandoned (possibly prematurely) after a suspected predation attack. This sheep carcass is partially articulated and retains some soft tissue (e.g. periosteum, tendon, muscle and skin/fleece). These bones had been collected for the purpose of analysis within days of the attack and cold stored. The bones of this individual are all fused, indicating an adult. The location of the attack was in a remote but grazed upland environment. The carcass could be categorised as fresh in that putrefaction had started (maggots) but was not advanced. The foal was totally disarticulated on arrival for analysis. The bones range from across the skeleton and are completely defleshed and dry. The individual is known to be a 3-month-old foal, and its juvenile status is attested to by the lack of fusion on the bones. The attack had taken place in an improved pasture land environment. There was a time lapse of several years between the attack and analysis, in which time the bones had been exposed to the elements, albeit in a shaded leaf-covered and, therefore, a partially protected environment. The remaining three partial sheep carcasses are in varying states of disarticulation. Two of these partial carcasses are articulated with fresh soft tissue attached, but no sign of putrefaction in one case (Carcass 3) and dried soft tissue in the other (Carcass 4). Carcass 3 is a juvenile of approximately 9 months and consists of mainly the cranial and limb material, lacking most of the vertebral column. Carcass 4, an adult, consists of a single articulated front limb. Both Carcasses 3 and 4 were collected soon after the attack, the former for the purposes of this analysis. The final sample, Carcass 5, is a juvenile, again approximately 9 months old and consists of a limited number of defleshed, dry and disarticulated bones that have been exposed since the suspected attack. These three animals were killed and their bones collected within close proximity of each other from an environment which is unimproved pasture land in remote upland.

3. Methodology

With the exception of two sheep carcasses which have bite marks (imperfectly) preserved on the skin, the analysis concentrates on the damage located on the hard skeletal tissue. The methodology includes a visual inspection of the bones by eye and by a low-powered light microscope. A cast, using dental impression material, was taken only where clear tooth cusps, crowns or scores could be identified. Vinylpolysiloxane impression material and/or putty was used to make a negative mould and pressed onto the bone surface. The requisite time was left for the material to set and then removed, leaving

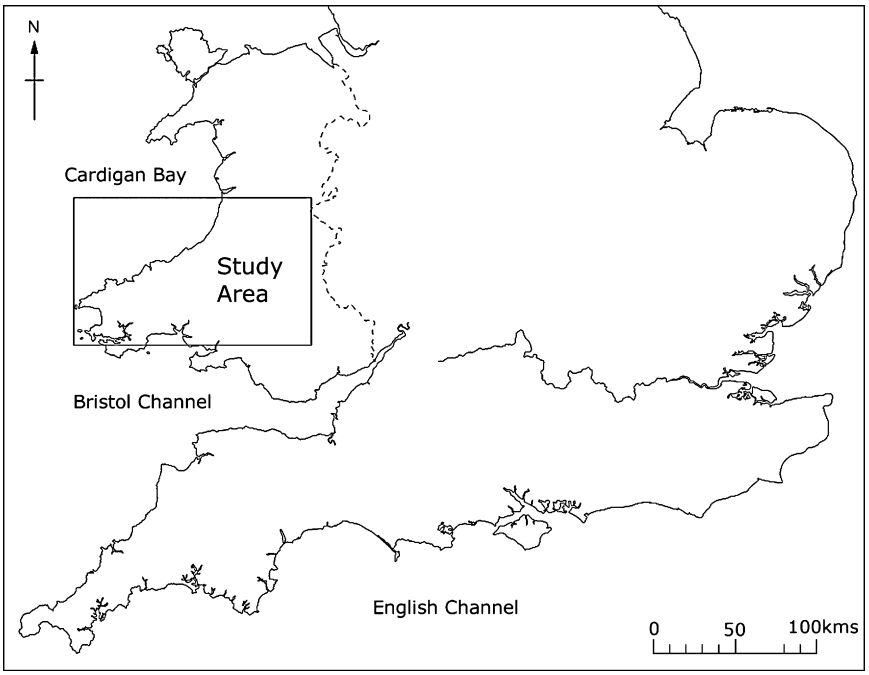

Fig. 1. Location of the study area within south-west Britain.

the pit or score impression in the dental material. Measurements of the length and breadth of the tooth pit and scores were made under a light microscope using electronic sliding callipers. Although not wholly in agreement with the definition, the accepted terminology of a score is given to any mark (i.e. grove or furrow) for which the length is three times longer than the width. Marks under this measurement include individual tooth cusps or crowns and are termed pits. Marks are recorded only if they are isolated or readily measurable. This has implications for Carcass 5 in particular. There are multiple pits on these bones but due to frequent overprinting not all are easily measured and hence, they are excluded from the analysis. All marks are combined and not restricted to and divided into long bone epiphyses and diaphyses, as (1) bones from across the skeleton are included in the analysis, (2) the majority of the samples are juvenile with lower structural bone density, and (3) both cancellous and dense bones surfaces show that the length and breadth correlation is sustained (Domínguez-Rodrigo and Piqueras, 2003).

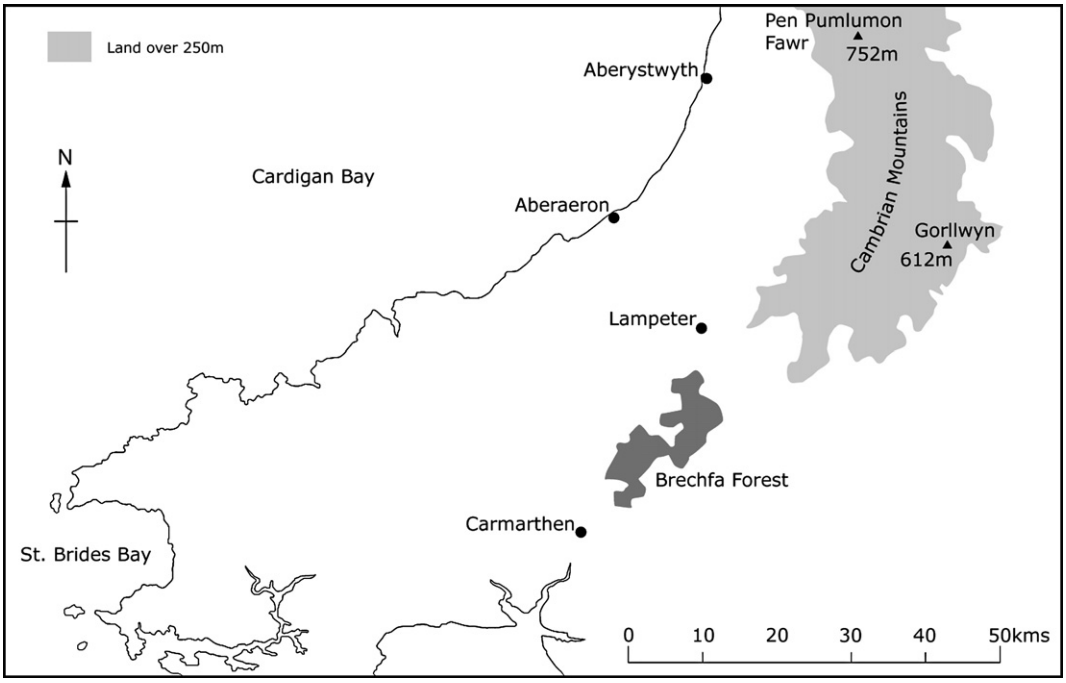

Fig. 2. Map of the study area in West Wales west of the Cambrian Mountains.

In addition to the casts of the bone surface, casts using similar dental moulding impression putty were taken of the upper and lower tooth rows from a range of comparative specimens. The dentition of leopard, puma and wolf were selected. Sufficient dental putty was combined to make a surface onto which the upper or lower tooth row (essentially half the dental arcade) was pressed flat. This results in the impression of the tooth row in the dental material and allows for the spacing between cusps of individual teeth or adjacent teeth to be measured. The technique was refined on a smaller scale using a just sufficient putty to take casts of the carnassial teeth. Separate casts of the carnassials were taken to enable better access and ease of movement when placed under the microscope. All measurements were taken under a low-powered light microscope using electronic sliding callipers.

4. Results

Although the relationship between length and breadth of the marks for both pits and scores are positive, they vary widely in strength (Table 1). The pit data show strong correlations and are all statistically significant. The score data are mixed in that they shows strong through to weak values not all of which are statistically significant. This supports existing data suggesting that tooth pits are, or should be, a more reliable indicator of carnivore taxa than tooth scores.

Pit length and breadth mean marks shown in Table 1 establish two groups. The first group consists of the mean pit length and pit breadth marks that fall near or under 1.5 mm length and 1 mm breadth, i.e. Carcass 5. The second group consists of those mean marks near or over 3 mm length and 2 mm breadth, Carcasses 1–4. The mean marks for the length: breadth ratio of tooth pits also show separation into group sizes and can be seen in Table 2. What is evident is that all carcasses have both small pits on all dimensional variables and narrow score marks. However, only Carcasses 1–4 show the medium to larger pits and/or wider scores indicative of modification by a medium- to large-size carnivore. Using these criteria Carcass 5 can be excluded as having been modified by medium to large carnivores.

Results show that the average number of marks per anatomical element is also variable but again supports a division (Table 1). Carcasses 1–4 all record nine or fewer tooth pit marks per bone with Carcass 5 recording 14. This is mirrored

Table 1
Sample size and score distribution of marks analyzed including the standard deviation (S.D.), confidence interval (C.I.), Pearson's coefficient (r)

	Pits		Scores	
	Length	Breadth	Length	Breadth
Carcass 1	$N = 30$		$N = 4$	
Ave. no. marks per element	7.75		1	
Mean	2.94	1.97	3.92	0.85
S.D.	2.85	1.90	3.04	0.46
95% C.I.	3.96–1.92	2.65–1.28	6.89–0.94	1.30–0.39
r	0.959		0.992	
Carcass 2	$N = 74$		$N = 16$	
Ave. no. marks per element	9.25		2	
Mean	4.62	2.54	8.08	2.03
S.D.	2.48	1.21	3.88	1.35
95% C.I.	5.19–4.06	2.81–2.26	9.98–6.18	2.69–1.37
r	0.846		0.868	
Carcass 3	$N = 20$		$N = 5$	
Ave. no. marks per element	2.85		0.71	
Mean	3.89	2.46	5.69	1.39
S.D.	3.67	2.10	2.57	0.69
95% C.I.	5.5–2.29	3.39–1.54	7.94–3.43	2.0–0.79
r	0.976		0.815	
Carcass 4	$N = 30$		$N = 14$	
Ave. no. marks per element	4.28		2	
Mean	3.86	2.55	5.21	0.89
S.D.	13.53	2.22	1.66	0.51
95% C.I.	8.7–0.98	3.34–1.76	6.07–4.34	1.16–0.62
r	0.948		0.295	
Carcass 5	$N = 28$		$N = 18$	
Ave. no. marks per element	14		9	
Mean	1.52	1.00	5.36	085
S.D.	0.96	0.45	2.21	0.35
95% C.I.	1.88–1.17	1.17–0.84	6.38–4.34	1.01–0.69
r	0.778		0.321	

in the score data with Carcasses 1-4 recording two or fewer scores per bone compared to an average of nine scores per bone for Carcass 5. The results suggest that Carcass 5 has suffered from more intense modification to the bone by a smaller agent than Carcasses 1–4 and that Carcasses 1–4 have different taphonomic histories involving medium to larger predators.

5. Discussion

The length:breadth ratios of these data are generally lower than those of existing published data (Selvaggio and Wilder, 2001) but do fall into the ranges already established with two main exceptions (Table 2). The first is that the mean scores indicating the largest predators (i.e. lions or hyenas) are not represented here even though large pits that do fall with their ranges are present. Secondly, a mean value representing the smaller carnivores extends the variation noted so far in experimental studies. The generally lower mean marks of the data are to be expected. The carnivores involved in the modification of this sample are unknown but are not expected to fall into the large-size carnivore taxa (lions, hyenas etc.) but into known indigenous smaller carnivore taxa such as fox and possibly medium-sized carnivore taxa including (allegedly) leopard. In this respect the tooth pit data are able to discern the largest or medium-sized carnivores from smaller carnivores. On the data presented here, with mean pit lengths and pit breadths of 1.52 mm and 1.00 mm respectively, large carnivores can be excluded as being active agents in the modification of Carcass 5, but remain a distinct probability in Carcasses 1–4.

This inference is supported by other evidence. Carcasses 1–4 all display large tooth pits in excess of 4 mm length and 2 mm breadth. These large tooth pits constitute between 27% and 57% of the marks preserved on the bones (Table 3). These dimensions have been highlighted (Domínguez-Rodrigo and Piqueras, 2003) as a means of differentiating the size of the carnivore acting on bone and, if robust, they do at least indicate intervention by a larger sized predator. A qualification is needed here in that size is relative. There is no suggestion here that the largest of carnivores (e.g. lion, hyena) are at work with this assemblage, even though there are some very large tooth pits that readily fall into their range. However, the carnivores responsible for these marks are much larger than the native predators. The mean marks for the tooth pit length (ranging from 2.92 to 4.62 mm) and breadth (ranging from 1.97 to 2.55 mm) of Carcasses 1–4 suggest some modification by a carnivore falling into a medium-sized carnivore category at least. Carcass 5 displays no medium to larger sized pits at all and the mean marks here suggest a much smaller size of carnivore. Although the collective data may support the intervention of a medium-sized carnivore in the cases of Carcasses 1–4, the data do not in themselves identify which one.

In itself the relationship between length and breadth, although it may be expected and where current research is focused, may not be particularly illuminating when applied to an archaeological sample. It may be correct to postulate that as a tooth gets longer it also gets wider, and this is supported in the tooth pit analyses of here and elsewhere. The same correlation in score mark data has been highlighted as being more equivocal. However, a similar relationship still may hold true to some extent, in that even though the tooth is being dragged over the bone to produce the score, a wider tooth will potentially make a wider score mark. In this respect score width may enable carnivore taxa to be distinguished, as in the case of an attack by a single large predator, a wide tooth making up the tooth pit also makes up the tooth score. Larger carnivores may leave wider or narrower pits or scores but small carnivores can only leave small ones. Correlations obtained from these data do show strong through to very strong correlations for Carcasses 1–3 (Table 1), indicating some relationship between the two variables. Score lengths here are observed to be limited by their location on any particular bone, in that larger surface areas preserve longer score marks than smaller surface areas. Hence the larger areas of cortical or cancellous bone can preserve potentially longer score marks than can the more irregular-shaped areas of the smaller juvenile vertebra, for example. Tooth size is not the only factor in determining the correlation of the component variables in tooth scores with regard to length of the score. Regardless of the factors determining the dimensional variables, score data remain less reliable as diagnostic indicators. This is not to say that they should be rejected altogether.

It does not take much to realise that a large pit (or a wide score) must have been created by a large predator but in order to better identify which predator, other approaches or combination of approaches are needed. Tooth cusps are most often observed as single or less frequently as groups of pits that may bear a spatial relationship to each other due to the morphology of the tooth crown. Where multiple cusps occur and are clearly part of a tooth crown or group of tooth crowns, measurements of the distance between the cusps of a single

Table 2
The mean length:breadth ratio of tooth pits ± 1 S.D.For Carcasses 1–5

Sample	*N*	Mean	±1 S.D.
Carcass 1	31	1.58	0.49
Carcass 2	74	1.84	0.53
Carcass 3	20	1.56	0.46
Carcass 4	30	1.54	0.55
Carcass 5	28	1.47	0.54

Table 3
Frequency and percentage totals of tooth pits with measurements over 4 mm and 6 mm length and 2 mm and 4 mm width

	Pit length			Pit width		
	4 mm	6 mm	%	2 mm	4 mm	%
Carcass 1	4	4	25.8	2	5	22.5
Carcass 2	26	18	58.6	32	11	57.3
Carcass 3	6	3	42.8	8	2	47.6
Carcass 4	5	5	32.3	7	6	41.9
Carcass 5	0	0	0	1	0	3.4

tooth or adjacent teeth can be made, the rationale being that consistently small pits close together are a better indicator of a small mammal than a large one. A large carnivore may make small pits but the spacing of the pits will be different, and this is related to the tooth morphology and dental configuration. The most frequently observed multiple pits are those of the premolar row with the (often) more pronounced mesial cusp producing a larger imprint than that of the distal cusp or the more evenly shaped and sized imprints of the cusps of the molars in the case of canids. Equally illuminating and where score data are useful is the spacing between individual tooth scores within a series of scores. Such scores are preserved as a series of parallel lines running in the same direction and are made as a result of a single event. Such scores may also be accompanied by smaller pit marks often made from the accessory cusps. Although rare, the measurement of one such case is presented in Table 4, where the recorded scores match the upper premolar and molar cusp pattern and spacing similar to that of a fox. This series of score measurements (here referring to the distances between the individual score marks on the bone) taken from a tibia of Carcass 5 supports existing evidence suggesting that this carcass shows modification by a small carnivore and that it closely matches a fox on the premolar/molar morphology and spacing. Similar conclusions can be drawn from the tooth crowns for which work is still ongoing but initially is proving successful in determining the intervention of this smaller carnivore. All carcasses have either cusps from a single crown or the distance between the cusps of adjacent crowns within the range of a small carnivore that, initially at least, closely match the fox. In one case, Carcass 1, the damage is very restricted and only observable on the scapulae: in other carcasses a wider range of skeletal parts are affected. Such patterning may yet hold clues to the behavioural activity of both the first and subsequent predators.

Attempting to match tooth marks with a medium-sized or large predator is more difficult but does remain a possibility. One problem is that a more powerful animal inflicts a good deal of damage to the bone. Extra bone may be pushed inwards and may form a more angular pattern on the bone and the subsequent impression material. This makes identifying the tooth cusp/s and the distances between the cusps more problematic. Attention here is focused on the three anterior cusps (protocone-parastyle-paracone) of the upper carnassial forming and preserving a tri-cuspid triangle pattern on the bone surface. Although imperfectly preserved in one case, another example shows a distinct tri-cusped triangle shape. Casts of tooth cusp patterning were compared to casts of the tooth morphology of the carnassials of the comparative samples. The measurements of both data sets are presented in Table 5 and the measurement points for the cusp distances are shown in Fig. 3. The distances between the tooth pits on the bone show measurements more comparable to the cusp distances of the carnassials of the medium-sized carnivores. They more closely fall in the size range of the puma and leopard than the wolf. Although the sample size is pitifully small, the cusp distance measurements do form a felid pattern. The cusp pattern is similar to the felids in that it does show a well-developed parastyle and protocone. It does not show the wolf pattern of the more anterior placement of the protocone and the lingo-labial (protocone to parastyle) relative narrowness of the wolf. Teeth of the carnivores are highly adapted. The blade-like adaptations of the carnassials to meat slicing and tearing or bone crunching have left a distinctive morphology in terms of the cusp pattern. The generally reduced protocone and the enlargement of the metacone-metastyle crest in all families (Hilson, 1990), and the relative development of the parastyle in felids makes for a distinctive tooth pattern. Identifying the distinctive cusp patterning may prove useful in determining a carnivore taxon responsible for predation. As yet the smallness of the study sample does not allow for any further exploration of the variability displayed in the medium-sized felids. It, therefore, remains unclear if the sample here is a different medium-sized felid species or a female displaying sexual dimorphism, a nutritionally stressed or simply a small variant of leopard.

Large and sometimes very deep pits, punctures and/or scores are evident on Carcases 1–4, signifying that at least a medium-sized carnivore is responsible in part for the modification of these carcasses. The cusp pattern preserved in Carcass 3 strongly indicates a medium-sized felid. Carcasses 1 and 4 have a single large and deep puncture in the proximal ulna. The damage to the superior surface of the olecranon indicates a single canine bite leaving a deep puncture in excess of a wolf and similar to the comparative felids in terms of size and shape (work on-going). In contrast to these large features all carcasses display pit and score patterns that imply smaller destructive agents have also modified these bones. In this respect the taphonomic overprinting can be determined. The cusp patterns preserved on Carcass 5 can eliminate carnivores much larger than a fox as taphonomic agents, although the extensive gnawing to the few surviving bones may well mask any previous activity.

Table 4
Measurements of the distance between tooth cusps of the upper dentition of fox and score marks taken from the tibia of Carcass 5

Measurement point	Sample	Fox
P3 to P4 paracone	10.38	10.12
P4 paracone to metacone	5.59	6.27
Metacone to m1 anterior cusp	3.73	3.66
M1 anterior cusp to M1 posterior cusp	3.54	4.14
M1 posterior cusp to M2 anterior cusp	3.06	3.36
M2 anterior cusp to M2 posterior cusp	1.85	2.85

All measurements in millimetres.

Table 5
Measurements of the tri-cuspid puncture marks from the radius of Carcass 3 and the anterior cusps of the upper carnassial of the comparative specimens

Cusp measurement points	Sample	Leopard	Puma	Wolf
Paracone to protocone	8.85	9.81	7.32	7.45
Protocone to parastyle	6.58	5.29	5.12	3.46
Parastyle to paracone	7.27	7.93	6.56	6.98

$N = 1$ for all samples. All measurements in millimetres.

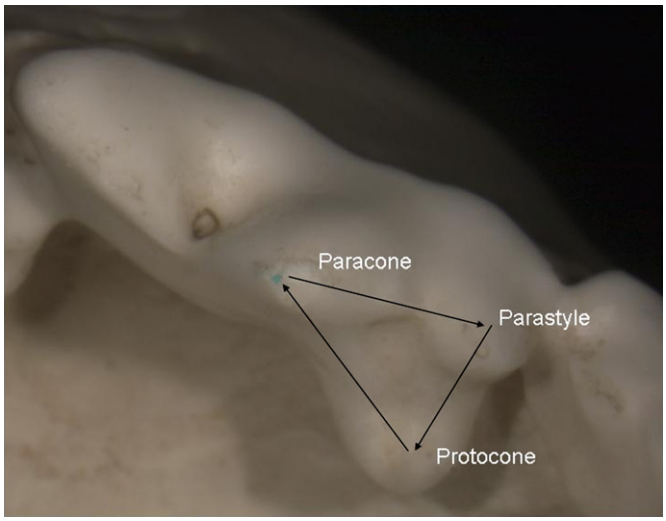

Fig. 3. Measurement points for the carnassial cusp distances. The tooth shown is the upper carnassial of puma.

In an archaeological context the identification of a particular carnivores involvement with an assemblage would rely on more than tooth pit data alone. A more complete taphonomic analysis would include skeletal part representation, element survivorship, location and patterns of damage, as well as contextual information regarding the depositional environment. Whilst a full taphonomic analysis is on-going it is evident from this analysis that Carcasses 1–4 do not fall readily into a canid (or hyaenid) pattern. The issue with modern sightings and alleged ''big'' cat attacks is the possibility that a large dog and not an exotic cat is the perpetrator. In the absence of any other independent or verifiable data, the individual tooth pit dimensions, tooth cusp distancing and patterning all strongly support the involvement of a medium-sized felid in the modification of four of these study carcasses.

This study broadly supports existing data on the usefulness of tooth pit measurements as a method by which past predation patterns can be explored. This research equally highlights the limitations of this technique, particularly if used in isolation. It adds to existing knowledge and contributes new data particularly with predation by smaller carnivores and on a wider range of skeletal elements. More importantly, it opens up and broadens the debate beyond tooth dimensions alone. Tooth pit dimensions are successful in determining a class size of predator but if used in isolation are insufficient to identify a particular carnivore taxon, whether in the recent past or relating to more distant predation events. Score data, although unhelpful and limited in some respects, are useful if they are preserved in a sequence that reflects the anatomical distinctiveness of the predator/s. These approaches can prove successful at identifying taphonomic overprinting and distinguishing the size range of the offending predators, if they are markedly different. If the size range of the predators is similar, more conclusive results and a more profitable approach would be to examine the individual cusp patterns and spacing of adjacent or related teeth. This study can only support previous pleas not to treat tooth pit data, in terms of size alone, in isolation.

Acknowledgements

I am grateful to the members of the public who contributed the carcasses for this study. My thanks go to Alayne Street-Perrott and Aleric B. Smith for some timely intervention, carcasses and insightful information. James Saunders provided advice on dentistry and impression taking. Sarah Jones and Hubert Wilson provided technical and drawing support, and the Department of Archaeology and Anthropology, Lampeter, for support and access to the faunal collections. I would like to thank the anonymous reviewers for their constructive comments.

References

Berger, J., Swenson, J.E., Persson, I.-L., 2001. Recolonizing carnivores and naïve prey: Conservation lessons from Pleistocene extinctions. Science 291, 1036–1039.

Boaz, N.T., Ciochon, R.L., Xu, Q., Liu, J., 2004. Mapping and taphonomic analysis of the Homo erectus loci at Locality 1 Zhoukooudian, China. Journal of Human Evolution 46, 519–549.

Carbone, C., Gittleman, J.L., 2002. A common rule for the scaling of carnivore density. Science 295, 2273–2276.

de Ruiter, D.J., Berger, L.E., 1999. Leopards as taphonomic agents in Dolomitic caves - implications for bone accumulations in the hominid-bearing deposits of South Africa. Journal of Archaeological Science 27, 665–684.

Domínguez-Rodrigo, M., 1999. Flesh availability and bone modifications in carcasses consumed by lions: Palaeoecological relevance in hominid foraging patterns. Palaeo 149, 373–388.

Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. Journal of Archaeological Science 30 (11), 1385–1391.

Dyan, T., Wool, D., Simberloff, D., 2002. Variation and covariation of skulls and teeth: modern carnivores and the interpretation of fossil mammals. Paleobiology 28 (4), 508–526.

Ginsberg, J.R., Macdonald, D.W., 1990. Foxes, Wolves, Jackals, and Dogs. An Action Plan for the Conservation of Canids. IUCN Publications, Gland, Switzerland.

Haglund, W.D., 1997. Dogs and coyotes: postmortem involvement with human remains. In: Haglund, W.D., Sorg, M.H. (Eds.), Forensic Taphonomy: The Postmortem Fate of Human Remains. CRC Press, Boca Raton, FL.

Hilson, S., 1990. Teeth. Cambridge University Press, Cambridge.

Lucas, A., 1997. Mammals in Carmarthenshire. Andrew Lucas, Dolgellau.

Meriggi, A., Lovari, S., 1996. A review of wolf predation in southern Europe: Does the wolf prefer wild prey to livestock? Journal of Applied Ecology 33, 1561–1571.

Mishra, C., 1997. Livestock predation by large carnivores in the Indian trans-Himalaya: conflict perceptions and conservation prospects. Environmental Conservation 24 (4), 338–343.

Oli, M.K., Taylor, I.R., Rogers, E., 1994. Snow leopard *Panthera uncia* predation of livestock: an assessment of local perceptions in the Annapurna conservation area Nepal. Biological Conservation 68, 63–68.

Ranta, E., Kaitala, V., Lundberg, P., 1999. A tale of big game and small bugs. Science 285, 1022–1023.

Roberts, D.H., 1986. Determination of predators responsible for killing small livestock. South African Journal of Wildlife Research 16 (4), 150–152.

Rothwell, B.R., Thien, M.S.D., Thien, A.V., 2001. Analysis of distortion in preserved bite mark skin. Journal of Forensic Science 46 (3), 573–576.

Selvaggio, M.M., Wilder, J., 2001. Identifying the involvement of multiple carnivore taxa with archaeological bone assemblages. Journal of Archaeological Sciences 28, 465–470.

Sinclair, A.R.E., Mduma, S., Brashares, J.S., 2003. Patterns of predation in a diverse predator-prey system. Nature 425, 288–290.

Stahl, P., Vandel, J.M., Rutte, S., Coat, L., Coat, Y., Balestra, L., 2002. Factors affecting lynx predation on sheep in the French Jura. Journal of Applied Ecology 39, 204–216.

Treves, A., Naughton-Treves, L., 1999. Risk and opportunity for humans coexisting with large carnivores. Journal of Human Evolution 36, 275–282.

Vogel, J.S., Parker, J.R., Jordan, F.B., Coury, T.L., Verino, A.R., 2000. Persian leopard (*Panthera pardus*) attack in Oklahoma. The American Journal of Forensic Medicine and Pathology 21 (3), 264–269.

Wilson, C.J., 2004. Could we live with reintroduced large carnivores in the UK? Mammal Review 34 (3), 211–232.